

EXPLOSIVE EVOLUTION OF PERENNIAL *ATRIPLEX* IN WESTERN AMERICA¹

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ABSTRACT.—New habitats opened up in western North America since the recession of Lake Bonneville and Lake Lahontan have admitted a host of new species of *Atriplex*. Every known evolutionary force is operating and at accelerated paces. Autopolyploidy appears to be more common than in any other reported group of plants. Natural hybridization between closely related species has provided a wealth of fertile segregants from which new adaptive types have been and are being selected. Hybrids between more distantly related species are sterile and some appear to have given rise to fertile allopolyploid derivatives.

All evidence points to a center of origin for *Atriplex* in northern Mexico. The numerous species which have migrated northward into western United States and Canada were apparently able to do so because attributes acquired to make them adaptive in the hot dry deserts of Mexico were characteristics which, uniquely, also pre-adapted them for colder climates and alkaline clay soils to the north.

Woody species such as *Atriplex canescens* and *A. confertifolia* hybridize rather easily with herbaceous perennial species such as *A. cuneata*, *A. gardneri*, *A. corrugata*, and *A. obovata*. Since most such hybrids are at least partly fertile and produce F₂ segregants of both woody and nonwoody types, the genetic basis for the accumulation of wood is apparently rather simple.

According to Antevs (1955), Broecker and Kaufmann (1965), Morrison (1965), Russell (1885), and others, much of the land surface of western Utah and northwestern Nevada was covered with ice and water as recently as 10,000-12,000 years ago. During the subsequent rapid disappearance of Lake Bonneville and Lake Lahontan and the attending desertizing of surrounding valleys, numerous salt playas and alkali flats were formed. Very few plants have been capable of surviving the severe physiological drought which characterizes such habitats. Compounded by attending severe climatological drought, which in many places is nearly absolute, the number of adaptive plants and animals is even further minimized. Indeed, in many areas, islands of dry, saline, mud hills and alkali playas are still completely uninhabited. Such areas represent some of

the few last frontiers on earth yet to be exploited by living organisms.

The principal pioneers which reach out farthest into these sterile desert islands are plants belonging to the family *Chenopodiaceae*. The entire family appears to possess, uniquely, characteristics which permit the accommodation of this double challenge of physiological and climatological drought. At the borders of every sterile, empty island in these saline deserts some member of this remarkable family is at the last frontier. In bottomlands it is usually *Sarcobatus* or *Suaeda* or *Salicornia* or *Allenrolfea*. On dryer sites it is *Grayia* or *Ceratoides* or *Atriplex* or *Salsola*.

Most chenopod genera are highly specialized with very few adaptive variables. Only two species of *Sarcobatus* have been described: *S. vermiculatus* (Hook.) Torr and *S.*

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baileyi Cov. There are only two species of *Grayia*: *G. spinosa* (Hook.) Moq. and *G. brandegei* Gray. There is only one species of *Ceratoides* (*C. lanata* (Pursh) J. T. Howell) in North America and one of *Cycloloma* (*C. atriplicifolium* (Spreng.) Coult.). But, in contrast, *Atriplex* is awesomely genetically rich, consisting of numerous species and varieties, many of which are still unnamed.

Some *Atriplex* species are very narrowly endemic, others are phenomenally widespread. *Atriplex navajoesis* Hanson is confined to a restricted area near Navajo Bridge in northern Arizona, whereas *Atriplex canescens* (Pursh) Nutt. extends all the way from Montana southward, deep into Mexico. Some species such as *Atriplex garrettii* Rydb. are remarkably uniform throughout their entire distribution; others, such as *Atriplex confertifolia* (Torr. and Frem.) S. Wats. are highly flexible with numerous ecotypes, chromosome races, and subspecies.

So genetically rich is *Atriplex* in western America and so new and variable are the environs which it occupies that we are permitted to witness the evolutionary process at an unprecedented rate. Every known strategy for speciation is evident, some of which, such as autopolyploidy, have never been reported to be nearly so significant in the evolution of other plant groups.

Interspecific hybridization followed by introgression, segregation, or allopolyploidy is common; mutations, drift, and autopolyploidy are found in nearly every species. Interpretations are easy in some groups, but in others the evidences are rather subtle and difficult to interpret.

EVOLUTIONARY HOT SPOTS

Atriplex is abundant throughout all of western America. One or more of the evolutionary forces can be witnessed in nearly every population, but there are a few particular sites where speciation is especially rapid.

One of the richest evolutionary sites lies in northeastern Mexico in a radius of about

200 miles around Monterey. Here there are numerous endemic diploid and tetraploid species, and numerous hybrid derivatives. As pointed out by Johnston (1941), *Atriplex stewartii* I. M. Johnston is an apparent derivative of the hybrid *Atriplex canescens* x *A. acanthocarpa* (Torr.) S. Wats. It has thin, broad leaves with undulating margins, much like the leaves of *A. acanthocarpa*, and four-winged fruits which, although diminutive, are much like those of *A. canescens*. West of San Roberto is another segregant from this hybrid but, in this case, with *A. canescens*-type leaves and *A. acanthocarpa*-type fruits. Even another derivative from this hybrid grows in very heavy gypsum soils southwest of Cuatro Ciénegas. It is much like *A. acanthocarpa* in many respects of habit and leaf but has a strong tendency for wings on an otherwise burrlike fruit.

Atriplex prosopidium I. M. Johnston is a handsome, tall, four-winged shrub with a deep blue cast which probably came from introgression of *A. obovata* Moq. into *A. canescens*. It is narrowly endemic to a small area around Monclova and Ocampo. A much more widespread putative derivative of this same origin covers thousands of acres south and west of Cuatro Ciénegas. It is a short-statured, heavy bush, much utilized by sheep and cattle in that area.

A second geographic center in which hybridization has played, and is now playing, a major role in the origin of new species of *Atriplex* is in north central Nevada. Valleys in this region run north and south between series of mountain ranges. Each valley is approximately 30 to 60 miles across and 100 to 400 miles long and usually opens up to common basins to the north and to the south. This peculiar physiography permits species to migrate from common populations into isolated valleys where independent speciation can occur and unique species can emerge. And they have. In almost every valley unique genotypes have become established. Furthermore, fortuitous contacts between north and south immigrants as well as fortuitous in-

roductions of particular combinations of species from either the north or the south has provided many of the valleys with new rich opportunities for interspecific hybridization followed by segregation, introgression, and polyploidy.

Atriplex canescens has been particularly contributive in this setting. In western Utah and northern Nevada it has hybridized with *A. tridentata* Kuntze yielding a host of new variables. This is particularly unusual because *A. canescens* in this area is tetraploid whereas *A. tridentata* is hexaploid. However numerous viable seeds are produced by the hybrid in nature, providing a host of segregating progeny. Some of these have recovered high fertility and chromosomal regularity at the tetraploid level but are phenotypically, and therefore genetically, strongly modified by *A. tridentata*. Conversely, some segregants have settled down chromosomally at $2n = 54$ and are phenotypically like *A. tridentata*, introgressed with *A. canescens*. Still others are not yet stabilized, either genetically or chromosomally. Each of these permutations have also been obtained in the experimental nursery at Brigham Young University from seeds collected from natural hybrids.

In and around Battle Mountain, Nevada, thousands of acres are occupied by a highly variable population of *Atriplex* which appears to have been derived from this parentage. The plants are strongly *A. tridentata* in many features but tendencies for winged fruits, earlier maturation, and woodiness all suggest introgression from *A. canescens*. This population appears to have become chromosomally stabilized at 27 pairs but is still unstabilized genetically.

In many of the valleys of west central Nevada, *Atriplex canescens* appears to possess genetic attributes of *A. falcata* (M.E. Jones) Standl. Since these *A. canescens* populations are hexaploid, whereas most others in western America are tetraploid (Stutz et al. 1975), and, since *A. falcata* has so far proven to be always diploid, these hexaploid *A. canescens* populations are prob-

ably allohexaploids derived from the hybrid of tetraploid *A. canescens* x diploid *A. falcata*. The principal difficulty with this interpretation, however, is the abundant variation within these hexaploid populations. A monophyletic hexaploid origin should have provided a very uniform product. Consequently, if the parentage has been correctly interpreted, then a polyphyletic origin is required, either initially or from among partially fertile segregants of the original hybrid or else abundant continuing hybridization between the new allohexaploid and one or both of the parents, followed by subsequent introgression.

Another highly variable hexaploid population occupies extensive valleys south of Eureka, Nevada. These are much less like *A. canescens* than are those described above which occupy valleys to the west. If these, too, are allohexaploid derivatives from the hybridization of tetraploid *A. canescens* and diploid *falcata*, considerable segregation must have occurred prior to the event of chromosome doubling because these plants show a minor influence of *A. canescens* and a major *A. falcata* input.

Certainty about whether or not these are the correct interpretations must await further study and experimental breeding. But whatever the ancestry, the fact remains that these partially isolated valleys in central Nevada are hot beds of *Atriplex* evolution. Nearly every valley possesses unique genotypes. In many valleys the variation is still rampant and has not yet settled down to a predominant adaptive theme. It is an evolutionary arena in which speciation is proceeding at unprecedented rates.

Eastern Utah is another region in which both polyploidy and interspecific hybridization have furnished many new species and varieties. The most common interspecific hybrids are those derived from *A. cuneata* A. Nels x *A. canescens* and *A. cuneata* x *A. confertifolia*. The latter is highly sterile but a few segregants are to be found in nature, and I have now obtained several seedlings from many thousands of hybrid "seeds."

The hybrid *A. canescens* x *cuneata*, however, is, in some places, quite fertile and produces extensive segregating populations. Immediately west of Hanksville, Emery Co., Utah, about thirty acres is dominated by hundreds of segregants from this parentage. Since *A. cuneata* is usually a suffrutescent shrub, dying back almost entirely each year to the ground, whereas *A. canescens* is a woody shrub, accumulating wood year after year, it was interesting to find both growth forms represented among the segregants, suggesting a rather simple genetic basis for this difference.

Numerous other natural interspecific hybrids have been found in eastern Utah, e.g., *A. confertifolia* x *A. garrettii*, *A. confertifolia* x *A. corrugata* S. Wats., and *A. confertifolia* x *A. canescens*, but extensive successful segregants have not yet been noted.

Probably the most significant products of interspecific hybridization in all *Atriplex* is that produced from hybridization of *A. canescens* with *A. gardneri* (Moq.) Dietr. In northern Wyoming and southern Montana these two species are often intimately sympatric. Hybridization between them is common, attended by a rich array of segregant products. From such hybrid swarms have come several highly adaptive combinations, one of which appears to be the widespread, herbaceous form of *A. canescens* which grows in the heavy clay soils on the banks of the Missouri River and its tributaries throughout most of Montana, southern Alberta, northern Wyoming and North and South Dakota. It was this form which was collected in 1804 by Lewis and Clark at Big Bend near Chamberlain, South Dakota, and which is the type for *A. canescens*. Because of the many differences which distinguish it from the typical taller, more woody, well-known four-wing saltbush of the Intermountain West and northern Mexico, a nomenclatural revision will be required.

ORIGINS

It is difficult to be certain of the center

of origin of species in a genus as genetically rich as *Atriplex*. According to Vavilov (1926), it would be in one of the areas in which there is abundant variation. However, in *Atriplex* this may not be a good index for origins. As pointed out above, most of the evolutionary hot-spots are of very recent vintage and possess abundant variation not because of antiquity but rather because of recent availability of new explorable habitats. Also, unacceptable are theories such as those of Matthew (1939) which suggest that centers of origins can be detected by the presence of advanced, progressive species. This, too, would place the center of origin in northern Utah and Nevada or eastern Utah, where evolution is currently explosive and where, but a few thousand years ago, much of the area was covered with water.

In view of the widespread severe ecological changes during Pleistocene and Holocene in all of western America north of Mexico, in view of the numerous affinities between perennial *Atriplex* species of northern Mexico and those to the north, and in view of the numerous species in southern states and Mexico such as *A. acanthocarpa* (Torr.) S. Wats., *A. obovata* Moq., *A. polycarpa* (Torr.) S. Wats., *A. hymenelytra* (Torr.) S. Wats., and *A. torreyi* (S. Wats.) S. Wats. which have no homologues nor even analogues in northern states or Canada and also because there is a paucity of perennial *Atriplex* species south of San Luis Potosi, northeastern Mexico appears to be the most likely area from which most contemporary perennial, North American species of *Atriplex* arose. Adaptation to the hot dry climate and gypsiferous soils of this area conceivably could have preadapted many forms for occupation of the xeric saline areas which became available to the north during late Pleistocene. It may have involved biological adaptation as simple as the capacity for accumulating and tolerating salts at an unusually high concentration. Ostensibly the attending high osmotic pressure of such an adaptation could function as an "antifreeze" in colder northern climates as well as a

mechanism for accommodating drought, both physiological and climatological. No other common denominator is yet apparent.

Such an origin is also fully supported by other lines of evidence. Leaves of all perennial *Atriplex* species, so far examined, have the "Kranz" type leaf anatomy which appears to be always associated with the C_4 photosynthetic pathway (Downton 1971, Polya and Osmond 1972). Even *Atriplex falcata* which now is confined solely to northern latitudes and other diploid species as far north as Edmonton, Alberta, still display Kranz type anatomy. If, as is generally maintained, C_4 photosynthesis is an adaptation to hot, bright desert conditions, (Downton 1971, Mooney et al. 1974, Smith 1976, and others) it is difficult to accept that these northern species arose *in situ* under existing climatic conditions. However, a southern hot-desert origin for a species now completely restricted to northern climates is also difficult to accept. But if the Kranz anatomy is as reliable an index to C_4 photosynthesis as has been claimed, and if C_4 photosynthesis is as restricted to hot climate plants as has been suggested, then there are really no other available explanations. And if we accept all of that then we are forced to accept, in either case, migration and evolutionary tempos of very unusual rates. The only apparent northerly migration lanes were right through Utah and Nevada, and these were mostly under water only 10 or 12 thousand years ago. If this migration were earlier, it must have been during the interstadial between the Bull Lake and Pinedale pluvials, and the current distribution of northern species as far south as northern Nevada and Utah would be a recent subsequent southerly migration.

Since most of Alberta and Saskatchewan was completely covered with ice and water as recently as 20,000 years ago (Bayrock 1969, Christiansen 1971), *Atriplex* species which are now restricted to areas in these provinces as far north as Edmonton and Peace River must have immigrated from the south since that time. Also, since consid-

erable time would be required for the wasting and disappearance of the ice sheets, desert conditions conducive to *Atriplex* migration would not have been available until even much later. And, since most of Utah and Nevada were still mostly covered with ice and water as recently as 10,000 years ago (Bissell 1963, Morrison 1965), there are not very many time periods left in which the required major desert could have developed. In fact, it appears that there are only two possibilities: (1) about 10,000 to 12,000 years ago, just prior to the last major Bonneville pluvial or (2) about 5,000 years ago during the Altithermal period of post Bonneville. In view of the great distance which migrating species would need to traverse to get from southern deserts to far northern latitudes, plus time for radiation into the numerous existing adaptive ecotypes and *in situ* synthesis of polyploid derivatives, neither of these time intervals are particularly appealing. But since there appears to be no available alternative it must have happened during one or perhaps both of these periods. The tempo of migration and evolution would have necessarily been very rapid. But since it is very rapid today, perhaps it is not so unrealistic after all.

According to Morrison (1965), a distinct period of desiccation separated the Bonneville and Draper pluvials about 12,000 years ago. It was a relatively brief period during which the Grantsville soil was deposited at levels as low as 4250 feet. This is just 50 feet above the current level of Great Salt Lake so would indicate desert conditions perhaps as severe as those existing today. Also Eardley (1962) found a huge bed of Glauber's salt ($Na_2SO_4 \cdot 10H_2O$) from 15 to 25 feet below the present-day bottom of Great Salt Lake, $9\frac{1}{2}$ miles across and 32 feet thick, the surface of which dated at $11,600 \pm 400$ years B.P. Further evidence of a major drought 10,000-12,000 years ago is furnished by cores taken from Searles Lake which show an 18-foot-thick layer of salt of that age (Smith 1962).

Increasing frequencies of *Atriplex confer-*

tifolia in wood-rat middens in the Mojave Desert beginning about 17,000 years ago (Wells 1976) may also be counted as evidence for extant desert conditions in western North America prior to the last Bonneville pluvial. Wells also furnished evidence which suggests that the Chihuahuan Desert may have originated less than 11,500 years ago. Widespread desert conditions may have lasted for only a few hundred or perhaps a few thousand years but were probably sufficiently extensive to permit *Atriplex* and other desert plants to migrate from the south.

Some of the *Atriplex* species which are now endemic to the northern latitudes are, uniquely, successfully competitive with grasses and forbs with which they grow. Elsewhere *Atriplex* is conspicuously a poor competitor and is successful on harsh sites primarily because nothing else can grow there. Consequently the northern forms have apparently become secondarily adapted for competitiveness in sites which are considerably more mesic than those occupied by other species of *Atriplex* further to the south. Since such adaptation is likely genetically somewhat complex, it probably required considerable time to arise. This is further argument that migration from the south must have occurred at an early period rather than during the Altithermal of only 5,000 to 6,000 years ago.

The pluvial period following the extant drought 10,000 to 12,000 years ago apparently wiped out all northern forms of *Atriplex* except those which were adaptively competitive with other mesophytes. At least one of these northern *Atriplex* species, near Edmonton, Alberta, is diploid so probably represents a product of primary evolution involving principally genetic drift and the acquisition of new adaptive mutations.

Considerable evidence is now accumulating which suggests that desert conditions were also widespread during the Altithermal period. Scott (1965) reports mollusks dated at 5500 B.P., buried 40 feet under eolian sand near Denver, Colorado, and Smith (1962) reports 40 feet of salt of altithermal

age deposited in Lake Searles in eastern California. Whether the warm Altithermal period developed synchronously throughout all of western America to provide one huge desert or whether deserts developed in different areas at different times is not known but neither is it critical to *Atriplex* evolution and migration. A single widespread desert would, of course, be simpler to comprehend but stepwise movement from one area to another could have been just as effective. The principle conclusion in either case is the same. *Atriplex* must have migrated from the south, over thousands of miles, across terrain which has subsequently become so modified that intervening forms have become completely extinct. Ancestral types, if they still exist, are so very different from those to the north which have evolved from them that evidences of such ancestry are not at all apparent.

Although the climate of northeastern Mexico has apparently changed very little during the past 30,000 to 40,000 years (Meyer 1973) in comparison to the tumultuous surface changes to the north, *Atriplex* growing there would have certainly continued to evolve. However, if the northern derivatives migrated from the south during the recent Altithermal period, many original ancestral types would predictably still be present. But none are to be found, a fact which suggests that migration must have been much earlier.

Wells (1966) has reported *Atriplex canescens* fossils at Burro Mesa in the Chihuahuan Desert which date at 36,000 years B.P. However, today only polyploid forms of this species have been found in Mexico (Stutz et al. 1975). The only population of diploid *Atriplex canescens* yet found is on sand dunes in central Utah and may represent the only relic stand of the ancestral form. However it is so genetically distinctive and so restricted in its distribution, it is almost certainly a derived form, considerably altered from its progenitors.

Many other diploid species of *Atriplex* scattered throughout the Intermountain

West are likewise geographically disjunct from any apparent Mexican relative. Most of them have narrow restricted distributions so were probably left behind as adaptations to unique situations during and after the migration rampage.

All of this argues strongly for greater antiquity in *Atriplex* migration than can be afforded by the Altithermal period and consequently supports other evidences for widespread desert conditions prior to the last Bonneville pluvial, of a magnitude sufficient to accommodate migration and evolution every bit as rapid as that which we witness today in the wake of new ecological sites exposed by post-Bonneville climatic changes.

As new ecological permutations now emerge, encroaching evolutionary fronts exploit them. Hence the entire Intermountain West today is once again an evolutionary arena in which new species are emerging and migrating at phenomenal rates. Mountains which are islands for mesophytes are isolation barriers for xerophytes, and the valleys which are isolation barriers for mesophytes are islands for the xerophytes. As these isolation barriers are surmounted by chance migrants, or adaptive deviants, new waves of evolutionary turbulence evoke yet other genetic permutations which accommodate even other challenges. It would be difficult to imagine a more dynamic arena wherein to witness the evolutionary process and it would also be difficult to find a genus better fitted for adaptively responding to it than *Atriplex*.

LITERATURE CITED

- ANTEVS, E. 1955. Geologic climatic dating in the west. *Amer. Antiquity* 20: 317-335.
- BAYROCK, L. A. 1969. Incomplete continental glacial record of Alberta, pp. 99-103. *In*: H. E. Wright, Jr. (ed.), *Quaternary geology and climate*. National Academy of Sciences, Washington, D.C.
- BISSELL, H. J. 1963. Lake Bonneville: geology of southern Utah Valley, Utah. *U.S. Geol. Surv. Prof. Pap.* 257-B: 101-130.
- BROECKER, W. S., AND A. KAUFMAN. 1965. Radiocarbon chronology of Lake Lahontan and Lake Bonneville II, Great Basin. *Bull. Geol. Soc. Amer.* 76: 537-566.
- CHRISTIANSEN, E. A. 1971. Tills in southern Saskatchewan, Canada, pp. 167-183. *In*: R. P. Goldthwait (ed.), *Till*, a symposium. Ohio State University Press, Columbus.
- DOWNTON, W. J. S. 1971. Adaptive and evolutionary aspects of C_4 photosynthesis, pp. 3-17. *In*: M. D. Hatch, C. B. Osmond, and R. A. Slayter (eds.), *Photosynthesis and respiration*. Wiley, New York.
- EARDLEY, A. J. 1962. Glauber's salt bed west of Promontory Point, Great Salt Lake, Utah. *Geol. Mineral. Surv. Spec. Stud.* 1: 1-12.
- JOHNSTON, I. M. 1941. New phanerogams from Mexico IV. *J. Arnold Arbor.* 22: 110-124.
- MATTHEW, W. D. 1939. *Climate and evolution*. 2d ed. New York Academy of Sciences, New York.
- MEYER, E. R. 1973. Late Quaternary paleoecology of the Cuatro Ciénegas Basin, Coahuila, Mexico. *Ecology* 54: 982-995.
- MOONEY, H. A., J. H. TROUGHTON, AND J. A. BERRY. 1974. *Arid climates and photosynthetic systems*. Carnegie Inst. Wash. Year Book 73: 793-805.
- MORRISON, R. B. 1965. Quaternary geology of the Great Basin, pp. 265-285. *In*: H. E. Wright, Jr., and D. G. Frey (eds.), *The Quaternary of the United States*. Princeton University Press, Princeton, New Jersey.
- PÓLYA, G. M., AND C. D. OSMOND. 1972. Photophosphorylation by mesophyll and bundle sheath chloroplasts of C_4 plants. *Pl. Physiol. (Lancaster)* 49: 267-269.
- RUSSELL, I. C. 1885. Geological history of Lake Lahontan. A Quaternary lake of northwestern Nevada. *U.S. Geol. Surv. Monogr.* 11: 1-288.
- SCOTT, G. R. 1965. Nonglacial Quaternary geology of the southern and middle Rocky Mountains, pp. 243-254. *In*: H. E. Wright, Jr., and D. G. Frey (eds.), *The Quaternary of the United States*. Princeton University Press, Princeton, New Jersey.
- SMITH, B. N. 1976. Evolution of C_4 photosynthesis in response to changes in carbon and oxygen concentrations in the atmosphere through time. *Biosystems* 8: 24-32.
- SMITH, G. I. 1962. Subsurface stratigraphy of late Quaternary deposits, Searles Lake, California, a summary. *U.S. Geol. Surv. Prof. Pap.* 450-C: 65-69.
- STUTZ, H. C., J. M. MELBY, AND G. K. LIVINGSTON. 1975. Evolutionary studies of *Atriplex*: a relic gigas diploid population of *Atriplex canescens*. *Amer. J. Bot.* 62: 236-245.

- VAVILOV, N. I. 1926. Studies on the origin of cultivated plants. Trudy Prikl. Bot. Selek. 16(2): 1-248.
- WELLS, P. V. 1966. Late Pleistocene vegetation and degree of pluvial climatic change in the Chihuahuan Desert. Science 153: 970-975.
- . 1976. Macrofossil analysis of Wood Rat (*Neotoma*) middens as a key to the Quaternary vegetational history of arid America. Quaternary Res. 6: 223-248.